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Density-dependent Processes and Management Strategy
for the Northwestern Atlantic Harp Seal

by

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Abstract

Density-dependent mechanisms are essential to the stability of the size of a natural population. Three such mechanisms, density-dependent age of whelping, pregnancy and pup mortality are modeled and investigated for the Northwest Atlantic harp seals. The variable pup mortality, although based upon minimal data, has a pronounced effect upon the shape of the sustainable yield curve. The maximum sustainable yield is estimated at 215,000 animals with 80% of this value being 0 class. The corresponding population size estimate is 1.4 million. These results are compared with previous estimates and others produced by varying the assumptions used to control the model population. The MSY population and yield are generally lower than estimates in models using fewer population-density controls.

INTRODUCTION

To study density-dependent mechanisms in wild mammal populations it is necessary to select species which have fluctuated widely during periods of intense biological sampling. The northwestern Atlantic harp seal (*Pagophilus groenlandicus*) is one such species (Sergeant 1976^a; Lett and Benjaminsen 1977). Although catch statistics are available for this population as early as the 18th century (Chafe et al. 1923) biological sampling did not begin until the early 1950's (Fisher 1952; Sergeant 1959; Sergeant and Fisher 1960). This was a particularly opportune time to begin sampling since the population was at high level, estimated as 2.3

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million (Lett and Benjaminsen 1977) following World War II.

The sampling initiated at that time has continued, and since 1960 at a more intense level (Lett and Benjaminsen 1977). In addition to catch at age information from the various fisheries, copious data have been collected concerning maturity, fertility (Fisher 1952; Sergeant 1966; Sergeant 1969; Øritsland 1971; Sergeant 1976_a) migration pattern (Sergeant 1976_a) feeding habits (Sergeant 1973_b; Kapel 1975) population census (Sergeant 1975; Lavigne et al. 1977) and mortality and sex ratios (Ricker 1971; Ulltang 1971; Benjaminsen and Øritsland 1975; Lett and Benjaminsen 1977; Lett et al. 1978).

Historically, harvesting levels on this stock have been particularly high. For example, during the period from 1830 to 1850 the offshore catch alone exceeded 450,000 pelts and reached a peak harvest level of 687,000 pelts in 1844. During the early 1900's the average catch was much lower about 150,000 pelts. The two Great Wars allowed for a stock recovery. After World War II hunting again became intense; the Norwegians joined the hunt and took large numbers of adult females which caused a dramatic decline in the stock (Lett and Benjaminsen 1977). Quotas were initiated in 1972 and the decline in stock numbers was halted. Since this time the stock has been increasing (Benjaminsen and Øritsland 1975; Lett and Benjaminsen 1977; Lett et al. 1977). However, the more important observation is that over the past 150 years this stock has maintained an average annual kill of 275,000 animals.

How has this population been able to survive for so long under such intense harvesting? The response to this, is the theme of this particular paper. Density-dependent mechanisms possibly operating at behavioral and physiological levels have given the stock resilience and stability in the face of widely varying annual exploitation. Indeed it is upon the knowledge of these density-dependent mechanisms that much of our management advice hinges.

The Stock

The harp seal, as a species, reproduces in three widely separated populations located on pack ice around Newfoundland, Jan Mayen Island and in the White Sea. Studies of skull and body dimensions (Khuzin 1963) have shown that the Newfoundland or western population, is more distinct from the two eastern populations than the two eastern populations are from each other.

There is limited cross over between the eastern and western herd (Sergeant 1976_a).

The Newfoundland population is divided into two sub-populations, one reproducing on the southward drifting pack ice, and forming up east of southern Labrador, the other in the Gulf of St. Lawrence (Fig. 1). The herd which forms up off Labrador, the Front, can further be divided into two subherds, sort of northern and southern contingents. The position of the whelping patches depends on the food supply and the formation of rather loose, rough ice interspersed with sufficient leads of water. At this time, March 8th or 9th, the younger animals which have less control over parturition than older seals, are hauling up to give birth. The older females remain in the area of abundant food for approximately two more days, then they too haul up and begin to whelp. This gives the impression of two subherds since the younger animals have drifted about 30 miles south by this time (Lett and Benjaminsen 1977).

In the Gulf of St. Lawrence whelping begins as early as February 22nd and continues until March 21st (Lett et al. 1977). The herd may split into as many as four subherds. Usually whelping begins on the ice edge along the Laurentian Channel around February the 22nd. This subherd then drifts south to the Bird Rock Islands just northeast of the Magdalen Islands. The period of whelping is protracted, however, the herd never seems to get much larger than 10,000 pups because animals are drifting out of the Gulf with the moving ice, as whelping occurs. Another subherd begins to form in the Bradelle Bank area, around March 3rd, west of the Magdalen Islands. This is the largest concentration of seals and is usually that which was exploited by the industry (Lett et al. 1977). Furthermore, before the Gulf was closed to hunting by large vessels in 1972 a subherd was exploited in the Northumberland Strait. Since the closure there have been no further reports of this subherd.

The only other subherd on record is that called the Mecatina Patch which forms up on the south shore of Labrador in the northern Gulf of St. Lawrence (Fig. 1). The whelping dates for this herd are similar to those of animals on the Front and they therefore may be part of the Front breeding colony. In former times this patch has been reported to have contained between 20,000 to 40,000 animals, however no proper census has ever been made. This is primarily due to the fact that there is no assurance that the herd will form up from one year to the next. Factors relating to the whelping of harp seals in this area are still unresolved.

Following the whelping period on the Front the seals move south into the vicinity of Notre Dame Bay on the northeast coast of Newfoundland (Fig. 1). By this time the pups have lost their foetal hair and are taking on the spotted juvenile appearance of "beaters". It is in this area that one of the major hunts occurs by Newfoundland landmen in small power boats and longliner vessels under 65'. In addition to beaters, large numbers of immature bedlamers and adults are taken, especially when these animals begin to concentrate on feeding shoals before their movement to the molting areas. Once the molt begins the animals swim north until they reach the floating pack ice usually in the area of the mouth of the Straites of Belle Isle. After molting which takes 3 to 4 weeks, the adults migrate to the Canadian Arctic.

The Gulf situation is somewhat different. The beaters and adults usually float out into the Cabot Strait, then begin to swim northward. Along the west coast there is again a substantial beater and juvenile fishery. Molting sometimes takes place in the vicinity of the Esquiman Channel (Fig. 1) but this is highly variable. The molting patch can be seen one day and gone the next with the seals swimming many miles to the south before they are sighted again. Within 3 to 4 weeks after the beginning of the molt the seals will have completely disappeared from the Gulf of St. Lawrence.

The beaters and juveniles following the northerly progression of the annual spring zooplankton bloom find their way to the west coast of Greenland (Sergeant 1976_b). By this time the mature and immature harp seals are fairly well segregated, with the matures mainly in Canadian high arctic. It is not known exactly why there is segregation but it is postulated by Sergeant (1973_a) that these younger seals feed on capelin (*Mallotus villosus*) and shrimp (*Pandalus* sp.) off west Greenland while adult seals concentrate on larger food items.

The distinctness of the Gulf and Front herds as separate breeding stocks and the degree of gene flow is interesting biologically, and important to the development of a realistic harvesting strategy. Sergeant (1977) presents detailed information indicating that there is substantial crossing over between the Gulf and Front of juvenile harps (79% age 1, 69% age 2, 11% age 3, and 0% aged 4 and older) but there is no indication of the intermixing of branded adults. It is known that seals that would normally have whelped in the Gulf do so on the Front when there has been no ice on

the Gulf (Lett et al . 1977) however these animals were identifiable as a distinct herd (per. comm. Tom Curran, conservation and protection officer, Goose Bay, Labrador). Thus the distinctness of the two breeding herds is still undecided. It is anticipated that research on genetic material from each herd conducted in 1978 will provide an answer to the problem (per. comm. David M. Lavigne, professor, Univ. of Guelph, Guelph, Ontario).

Age Composition Data

Certain vital rates are important in the assessment of any animal population (Lett and Benjaminsen 1977). Usually the instantaneous mortality rate is determined by analysis of catch-at-age data making the assumption that population and catch structures are the same; however, this assumption can lead to large errors in the instance of the northwestern Atlantic harp seal population (Benjaminsen and Øritsland 1975).

Catch-at-age data form the basis of the assessment of most animal stocks. The determination of the real catch-at-age structure is a formidable problem in itself for this fishery since it is very diverse. The problem consists of producing a weighted age frequency of the total annual catch for 1-yr-old and older seals (1+), which amalgamates the catch frequencies from the individual fisheries in their proper proportions (Table 1).

Samples of seals shot in Notre Dame Bay, Newfoundland, consist primarily of animals that have not fully developed their mature markings, known as bedlamers. The La Tabatiere, Quebec and Labrador net fisheries yield samples of pregnant females and mature males as they migrate south into the whelping areas. Samples taken in this area during January however, show a preponderance of seals mature for the first or second time since these animals arrive later than the older ones. Shot samples recovered from St. Anthony, Newfoundland seem to better represent the population age structure. Statistics breaking down the catch into these individual areas are not always available on the same scale as the sampling, however when data are available they indicate that on average each of these fisheries tends to be roughly equivalent in overall catch. Therefore the catch frequency is summed without weights to produce a catch composition for the overall landmen catch without serious error (Lett and Benjaminsen 1977, their table 1).

The large ships' catch from the breeding areas and molting patches, is considerably different than the catch structure from the overall landmen

sample and therefore must be treated separately (Lett and Benjaminsen 1977, their table 1). In these samples there is usually a high representation of one and two year old animals, basically because these animals are segregated around the periphery of the adult herd and are more easily accessible to hunting. The overall landmen catch composition must be combined with that of 1+ animals exploited by large vessels giving a weight to each frequency in accordance with the catch. If this procedure is not followed, a serious consistent bias would result, especially in the last 15 years due to the exponentially increasing interest of Newfoundland landmen in the fishery (Lett and Benjaminsen 1977, their fig. 2).

Between 1952 and 1960, jaws of seals for age determination were collected on a regular basis from the landmen's catch and this sector of the hunt can be considered well represented (Sergeant and Fisher 1960; Sergeant per. comm.). During 1952-54 and 1957-59 samples of jaws were also collected from large vessels. However, the 1957-58 samples are sparse and it is unlikely that they accurately represent the catch. For this reason the years 1955-60 were replaced by average catch-at-age frequencies for large vessels. The attendant errors are possibly serious since during this period the large vessel hunt on 1+ animals represented between 87.5 and 95.5% of the total catch (Table 1).

In 1961 sampling began to steadily improve with both the large vessel catch from the molting patches and the landmen's catch being well represented. Annual catch-at-age samples from 1961 on came from a number of sources (Sergeant 1971, 1972, 1976 per. comm.; Øritsland 1971; Benjaminsen and Øritsland 1975). A good sample was not taken for either the landmen's or large vessel catch in 1972, but the available data were including in ensuing analysis. The samples from 1967 on seem to have improved, except for 1972.

Samples of the Greenland and high Arctic hunt, representing 8% of the total catch on average, are excluded from this analysis from 1952 to 1975 since no consistent sampling and catch records are available.

Shot samples of males from the molting patch are used to determine some estimates of natural mortality. One of the primary problems is the fraction of 1-yr-old seals in the sample. As pointed out, this age-group is usually segregated from the remaining age-groups and is not consistently sampled at the molting patch (Benjaminsen and Øritsland 1975). Furthermore,

the hunt closing date also affects this sample; the earlier the hunt in the molting patches is terminated, the fewer females are represented in the catch (Sergeant 1965; Øritsland 1971). Thus the mature age composition varies depending upon the length of hunt and consists mainly of males. At age two the sex ratio is about 50:50 but by age 10 about 80% of the molting animals are male (Fig. 2). This is primarily due to the females remaining in the water and feeding to regain the energy lost during whelping and suckling. As the females gradually fatten they begin to haul out onto the ice flows.

DETERMINATION OF BIOLOGICAL RELATIONSHIPS AND ESTIMATION OF PARAMETERS

The Instantaneous Rate of Natural Mortality, M.

The most elusive vital rate in population dynamics is usually natural mortality. Since the exploitation rate of 1+ seals is very low, currently about 0.015 (Lett et al. 1977), the annual 1+ deaths are primarily due to natural mortality.

Natural mortality was estimated using pup productions (Benjaminsen and Øritsland 1976) determined by the survivorship index method, (Benjaminsen and Øritsland 1975, Sergeant 1975), information on maturity, sex ratio, pregnancy rate, and the population structure of seals in the molting patches. The analysis assumes that there is no difference between the natural mortality rates of male and female harp seals. The validity of this assumption is based upon the observation that the female harp seals have similar growth rates and achieve equivalent maximum rates (Sergeant 1973_a). The metabolic rate and body size of seals is well correlated (Lavigne et al. 1976), and since the mortality and metabolic rates of animals are related (Simms et al. 1959) it is unlikely that male and female harp seals have different natural mortalities.

The population structure was determined from large vessel catches in the molting patches as given in Lett and Benjaminsen (1977) and Sergeant (1977). These catches were multiplied by the fraction of males at different ages (Fig. 2) to give an estimate of the population structure of 2+ animals. However, partial recruitments annually vary to some degree among the younger age-groups, therefore, only animals aged 5 to 22 were used to calculate natural mortality.

By knowing the maturity, sex ratio, pregnancy rate and population structure, the pup production could be broken out over the appropriate age-groups to give

estimates of numbers-at-age. We assumed, as Lett and Benjaminsen (1977), that 6% of the breeding females are over the age of 25. Thus, M can be simply calculated for each age-group using the formula,

$$M = \ln \left(\frac{N_{a,t} - C_{a,t}}{N_{a,t+1}} \right) \quad (1)$$

where $N_{a,t}$ is the numbers-at-age at year t and

$C_{a,t}$ is catch-at-age for year t.

This gave an estimate of $M = 0.10$ with a S.E. of 0.03 between 1966 and 1977 for age groups 5 to 22. The maturity was estimated by linearly interpolating the 1966 and 1977 reported ogives. Sampling for ages over 22 was erratic and produced results in which we could have no confidence.

Using a method devised by Ricker (1971), Benjaminsen and Øritsland (1975) calculated natural mortality to be 0.102 with a 0.011 S. E. A new consideration of these data has modified this estimate to 0.106 (ICNAF 1977). Lett and Benjaminsen (1977) estimated natural mortality to be 0.114 by a rather suspect method while Winters (1976) estimated natural mortality to be 0.115. Earlier estimates of natural mortality were somewhat different. Both Ricker (1971) and Ulltang (1971) estimated natural mortality at about 8% per year. Sergeant and Fisher (1960) determined estimates of total mortality between 1952 and 1954 as low as 0.079. It can be seen from all these estimates however, that natural mortality for harp seals is near 0.10 and that this value may be conservative.

In our analysis we could find no evidence for age dependent natural mortality which is not surprising considering the uncertainties in the data and delicate changes possibly exhibited by this parameter (Lavigne *et al.* 1976). However, more detailed data of this kind exist for harp seals than perhaps any other large mammal stock, thus an assumption of constant mortality for 2+ age animals is quite justifiable based upon the analysis.

An important management consideration would be mortality in the first year and whether it varies in relation to some density-dependent mechanism as Lett and Benjaminsen (1977) have suggested.

Sequential Population Analysis

Sequential population analysis is a method of estimating the number in a

population by age for an interval of years from aged catch data (Fry 1949; Murphy 1964; Jones 1964; Gulland 1965; Pope 1972). The analysis of a year-class starts with an estimate of the number alive in the last year for which catch data on that year-class are available (terminal year-class size) and builds estimates of numbers in previous years by adding estimated loss due to hunting and natural mortality each year (Fig. 3). Inputs are thus the catch data, an estimate of natural mortality and estimates of the terminal year-class sizes. For the harp seal population the catch-at-age for 1952 to 1977 and age 1 to 25 and a natural mortality of 0.1 were used. Estimates of the size of the 1952 to 1976 year-classes in 1977 and the 1927 to 1951 year-classes at age 25 were needed. For the harp seal population the numbers-at-age are calculated at the time of whelping (just before the hunt). Since most of the hunt takes place shortly after whelping it is assumed that the hunting mortality is instantaneous and independent of natural mortality. Thus the numbers-at-age according to the following equation:

$${}_{a+1}N_{t+1} = ({}_{a}N_{t} - {}_{a}C_{t}) \cdot \text{EXP} (-M) \quad (2)$$

which corresponds to the assumptions in Pope's (1972) cohort analysis. Since the analysis works backwards from the oldest age, this equation is used in the following form:

$${}_{a}N_{t} = {}_{a+1}N_{t+1} \cdot \text{EXP} (+M) + {}_{a}C_{t}. \quad (3)$$

For each succeeding estimate the size of the year-class is increased to account for natural mortality, then the catch is added.

Terminal year-class sizes can be estimated either directly or by using an estimate of the exploitation rate to calculate the year-class size from the catch data. For year-classes 1951-1976 it is possible to estimate the year-class sizes in 1977. For year-classes 1926-1950 exploitation rates at age 25 were estimated. The population structure in 1977 can be estimated by applying the sex ratios on the molting patch to the 1977 molting patch sample taken in the large vessel catch. If sex ratios in the population, pregnancy rate and whelping ogive are known than this population, pregnancy rate and whelping ogive are known then this population structure can be used to calculate the population size required to give any particular number of pups. With an estimate of the latter, numbers-at-age in 1977 can be estimated and hence, terminal year-class sizes for year-classes 1951-1976.

It is harder to estimate terminal exploitation rates for the other year-classes. These were developed by the following iterative method. First it was assumed that the selectivity of 25 year olds in the hunt had not changed relative to the selectivity of all seals over the age of 10. Thus the ratio of the exploitation rate on 25 year olds to the average exploitation rate on 11+ seals was kept approximately constant from 1952 to 1977. Once numbers-at-age are estimated, pup productions can be estimated for each year, as was done in 1977. If there were an independent estimate of pup production the exploitation rate on 25 year olds can be adjusted until the two estimates agree. The other estimate used was derived by Winters (unpublished data) from survival indices. The Y on X regression values were used since the X variable (pup catch) probably has a much smaller relative variance than the Y variable (survival indices). These values are shown in Table 2 with 90% confidence limits on two of the points

For the calculation of pup production, the sex ratios in the population derived in Lett and Benjaminsen (1977) were used. Pup production in 1977 was assumed to be 330,000 which is in the range of values that were agreed upon as being most realistic at the CAFSAC¹ Marine Mammals Subcommittee meeting in October 1977.

To derive an initial set of numbers a pregnancy rate of 0.92, mean age of whelping of 4.5 and the whelping ogive derived in Lett, et al. (1977) were used. The exploitation rates on 25 year olds were then adjusted as discussed above. With this set of values, density-dependent functions for mean age of whelping and fertility rate were derived and the analysis was repeated until the results stabilized. The pup productions of Winters (Table 2) were not reproducible using the assumed starting population structure in 1977 without extreme variation in exploitation rates. The population structure was therefore altered slightly to increase the proportion of older seals. Twenty-five year olds were increased by 10%, 24 year olds by 9.6%, 23 year olds by 9.2%, et. The proportions were then renormalized to add to 100%.

Final numbers-at-age are shown in Table 3 and the estimated pup production is shown in Table 2 and Figure 3 and they do not show the amount of variation exhibited by Winters' data but follow the same trends. The exploitation rates

1. CAFSAC is an abbreviation for Canadian Atlantic Fisheries Scientific Advisory Committee.

on 25 year olds and the averages for 1+ and 11+ seals are shown in Table 4.

To develop the density-dependent functions a 1+ population estimate was needed for 1947. There are 1+ catch data but no aged samples for 1947 to 1951. These were aged with the 1952-1956 average and these years were added to the analysis for one run to produce the 1947 point.

A word of caution should go with these sequential population estimates. This sort of analysis uses all the input data to estimate the required numbers and there are no degrees of freedom to estimate error. Confidence limits on the estimated pup productions used to adjust the exploitation rates were shown. The sample on which the population structure is based comprised fewer than 1500 animals and most of these were less than 6 years old. Exploitation rates on 1+ animals are very low, and hence as noted in Pope (1972) even though the catch data are probably quite good the initial estimates are not corrected very much. Hence the resultant best estimates of the numbers-at-age in the population should also carry sizeable confidence limits. However, there is an overall consistency in the results giving confidence to the estimates of total population and population trends.

Density Dependent Mortality in the First Year

Estimating pup production by cohort analysis gave more erratic results (Lett and Benjaminsen 1977, their fig. 3), than would be expected for a marine mammal population. It was postulated at this time that perhaps this variation was attributable to a fluctuating natural mortality rate of pups which in some manner responds to exploitation.

The existence of a density-dependent mortality relationship was investigated using the numbers of age one animals from our sequential population analysis and estimates of the number of pups from application of the maturity ogive and pregnancy rate to the sequential population analysis population estimates. Escapement was determined by subtracting the catch from the pup abundance estimates from 1950 to 1976. The natural mortality of pups, M_0 , was then calculated using the following equation,

$$M_0 = \ln \frac{ESC}{N_1} \quad (4)$$

Where ESC is the escapement and N_1 is the abundance at age one from sequential population analysis. Due to the high variability in the estimates from year to

year values were averaged over 5 year periods.

<u>Period</u>	<u>Escapement \pm 1SE</u>	<u>Mortality \pm 1SE</u>
1952-56	319.2 \pm 30.3	0.48 \pm 0.11
1957-61	344.2 \pm 25.3	0.50 \pm 0.14
1962-66	150.6 \pm 20.5	0.07 \pm 0.22
1967-71	137.8 \pm 19.9	0.09 \pm 0.09
1972-76	197.6 \pm 10.6	-0.08 \pm 0.05

It is clear from this analysis that there has been a significant drop in natural mortality that seems to be related to escapement (Fig. 6).

However, because of the way the points are spaced, it is impossible to tell the exact nature of the relationship. One hypothesis may be a continuous response, while another may imply a sort of step function. The response presented here (Fig. 4) is a compromise between the two. Furthermore, it is interesting that the average mortality, $M = 0.2$, is twice that of 1+ seals. This is the exact level proposed by Lavigne et al. (1976) for 0 group animals.

Are these estimates real, or simply anomalies of the manner in which the data were analysed? Our opinion is that this is a sound relationship. It is only for values prior to 1962 that a continuous relationship exists. The 1962 year-class is 15 years and older in 1977 where there may be a problem with the initial estimation of numbers at age. This error could be the result of a severely biased sample of molting animals; since it is unlikely that errors in the sex ratio, or maturity ogive would have much effect. Furthermore, it is difficult to see how a consistent bias in sampling could result in such an abrupt change between the periods 1957-61 and 1962-66.

Density dependent mortality in the first year has been shown for grey seals (*Halichoerus grypus*) breeding at the Farne Islands (Bonner 1975) and for the northern fur seal (*Callorhinus ursinus*) (Lander and Kajimur 1976). The most important cause of death of the young grey seal ashore is starvation. This occurs when the bond between mother and young is broken and the juvenile animals become separated from their food supply (Bonner 1975). Given the analysis that has been done here, this mechanism cannot be hypothesized for harp seals since the escapement occurs following the beater hunt long after the animal has been weaned.

Mortality among the northern fur seals has been related to higher densities on land, resulting in an increased incidence of hookworm. Apparently

some critical mean density of animals is necessary before the parasitic infection reaches epidemic levels (Lander and Kajimura 1976. These cause internal hemorrhaging, weakening and eventual death. Furthermore, there is some speculation that weakened animals are less able to survive oceanic storms.

With virtually no knowledge of parasitic infections in harp seals it is difficult to hypothesize a similar mechanism. The only hypothesis we can think of involves food and the rigors of the first northerly migration. O-group seals feed mainly on euphausiids in the surface layers during their stay off the northeast coast of Newfoundland and during their migration to Greenland (Sergeant 1973; H. Fisher per. comm., Professor, Univ. of British Columbia, Vancouver). Before the migration north the seals form feeding concentrations (T. Curran per. comm). Possibly competition at this time for a limited food resource results in some seals being unfit to make the long migration northward. Sergeant (1973) noted that very small juvenile seals did not attempt to migrate and therefore become separated from major supplies of food. Lavigne et al. (1976) observe that lean seals have a higher metabolic rate than fat seals. Thus any density-dependent mechanism resulting in a leaner seal would have an enhanced effect on the animal's physical state, since more and more of its energy reserve would be required to simply maintain a constant deep body temperature and less could be put into the gathering of food. This vicious circle would probably lead to death. Perhaps this is the reason for the discontinuity between points before and after 1962.

Given the level of knowledge on this subject, there are probably a dozen equally plausible theories. For now it is merely enough to say that a relationship seems to exist and more research is required for its validation.

Density-Dependent Age of Whelping

For female harp seals the current stage of maturity can be judged by examination of ovaries for the presence or absence of a new *corpus luteum*). This structure is obvious well before the time of implantation of the embryo, an event that is delayed several months in seals (Sergeant 1973). While the presence of a *corpus luteum* does not necessarily indicate a successful pregnancy, it indicates that maturation of a follicle has taken place. Øritsland (1971) has used the back calculation of *corpus albicans* as an indication of the age of sexual maturity. This technique can be misleading in that these small scars can be readily missed, and persist only for a few years, perhaps 3 - 4 years for

harp seals (Sergeant 1973_b).

It is possible that the mean age of maturity has varied over the years, in addition to the standard deviation of the ogive. Variation in the standard deviation was checked by standardizing all the ogives to zero mean age and looking for inconsistencies in the rate of accumulation of mature animals within the population. Since all the ogives superimposed one another it was concluded that the standard deviation was not varying.

Cumulative normal distributions and Arc sine transformations were used to linearize the data in different years. It was found, in accordance with Lett and Benjaminsen (1977) that the Arc sine transformation, using a range of 0° to 90°, gave the best fit to the data:

$${}_t E_a = \text{Sine}(31.34 + 19.91 \times a) \quad (5)$$

Y on X regression of

Arc,sine ${}_t E_a$ on 'a

$$R^2 = 91.75$$

$$F = 133.41$$

where ${}_t E_a$ is the fraction whelping at age a in year t.

The point of 50% maturity was interpolated from the various curves in different years and regressed against 1+ population sizes lagged for different annual intervals to see which gave the best fit. The lag producing the highest correlation was 5 years (Fig. 5), thus the equation that was developed to describe shifts in the mean age of whelping, \bar{A} , was,

$$\bar{A} = 3.875 + 9.126 \times 10^{-7} \text{POP}_{t-5} \quad (6)$$

Functional Regression

$$R^2 = 90.09$$

$$F = 20.44$$

$${}_t E_a = \text{Sine}(31.34 + 19.91 \times a - (3.875 + 9.126 \times 10^{-7} \text{POP}_{t-5})) \quad (7)$$

Sergeant (1966, 1973_b) first proposed that the mean age of maturity was a density dependent relationship. Indeed this phenomenon is known for other marine (Gambell 1973) and terrestrial mammals (Markgren 1969). Lett and Benjaminsen (1977) developed a mathematical relationship for harp seals. Laws (1956, 1959) noted that in Phocidae, sexual maturity is attained at a

constant proportion of the final or asymptotic body growth (about 87%) and it is attained at an earlier age when growth is accelerated.

Assuming that the growth rate of juvenile seals is stock dependent in a similar manner to the mortality rate, this would provide a mechanism for density-dependent maturity. The 5 year lag then, is certainly consistent with Law's observations.

Density-Dependent Fertility Rate

Density-dependent fertility was first noted by Lett and Benjaminsen (1977). There have been complaints from time to time that more estimates are available, and that no differentiation between Gulf and Front samples is made. Therefore, we present all the available data (Fig. 6) in the literature,

<u>Location</u>	<u>Year</u>	<u>Estimate of fertility rate</u>	<u>Reference</u>
Front	1953	89.0	Sergeant (1966)
	1964-67	92.1	Øritsland (1971)
	1968	95.5	Sergeant (1969)
	1968-70	97.8	Sergeant (1976)
	1976	95.4	Sergeant (1976)
Gulf	1951-54	86.0	Sergeant (1966)
	1952	80.0	Fisher (1952)
	1964	84.0	Sergeant (1966)
	1965	90.0	Sergeant (1966)

and compare with current estimates of 2+ population size there is a fairly clear density-dependent relationship (Fig. 8). The data were plotted against the 2+ population size since the younger animals remain segregated from the herd and may not compete for available resources. Data for the same year for both areas were combined and the following best fit was derived:

$$PR_t = 102.297 - 7.3734 \times 10^{-6} \cdot (2 + Pop_{t-1}) \quad (8)$$

Functional Regression

$$R^2 = 68.69$$

F = 6.58 significant

where PR_t is the pregnancy rate in year t,

t refers to the year in which the pups are produced,

$2 + Pop_{t-1}$ is the 2+ population the year before (the year they became pregnant).

Variable fertility rates are well known and have been observed in at least three populations of whales (Gambell 1973). In addition, an unexploited population of Antarctic crabeater seals (*Lobodon carcinophagus*) which, like harp seals enjoys an unlimited ice substrate on which to whelp, has a low pregnancy rate of 0.76 (Øritsland 1970). Margen (1969) found that the ovulation rate in moose (*Alces alces*) was related to factors such as age, body size, nutrition and population density. Indeed it is well known that fertility varies markedly in managed, utilized deer herds (*Odocoileus virginianus*). Nazarenko (1975) presents data on the White Sea stock of harp seals indicating the fertility rate there is only about 69%. The reason for the discrepancy between the two populations is unclear.

CONSTRUCTION OF THE SIMULATION

The structure of the model is shown schematically in Figure 7. A detailed description follows from which one could reconstruct the actual computer program. This program, which has evolved from the APL listing given in Lett and Benjaminsen, (1977) allows the user to estimate the population as specified by sex, age and membership in the Gulf or Front subherd.

The starting population is separated into male and female populations for the Front and Gulf. The fraction for Front and Gulf split was 68:32 for all initializations. Sex ratios for both Front and Gulf were initialized as shown in Table 5. The sex ratio of the large vessel catch in the front followed the distribution given in Table 5 and the sex ratio of the large vessel catch in the Gulf was assumed to be 50:50. These steps correspond to the block labeled "Initialize parameters" in Figure 7.

The age distributions of the catch are based on those reported in Lett and Benjaminsen (1977) except for the landsmen and large vessels catches in the Gulf. These two distributions were compiled from data from the La Tabatière fishery from 1952 to 1960.

Catch distributions are used to decompose the input catch levels (Table 5). They were the same for all simulations. The 1+ catches except for the large vessels were simulated to be "stochastic". By stochastic it is meant that the user of the model has the option of allowing these catches to be drawn from a normal distribution whose mean is given as an input and whose standard deviation

is 40% of that mean or given by the user. The coefficient of variance of 40% was chosen to approximate the data reported in Lett and Benjaminsen (1977). If only one run is made using this model the catches are constrained to the means of the distributions. If two or more stochastic runs using a given set of catch level inputs are run, the catches are chosen from their respective distributions and appropriate statistics are compiled. This arrangement was introduced to allow estimates based on the means alone as well as those containing the variances associated with these levels. The normal distribution was simulated on the computer by using the Muller (1958) transformation on random numbers uniformly distributed between 0 and 1 supplied by a FORTRAN sub-routine. This transformation is

$$Z = -2 \ln (U_1) \cos (2\pi U_2) \quad (9)$$

where U_1 and U_2 are "random" numbers

The Z has a zero mean and unit standard deviation. In order to have the desired mean, m, and standard deviation, s, the Z is scaled into Z' as follows:

$$Z' = m + sZ \quad (10)$$

The large vessel catch was modeled without a standard deviation but could be specified as a given catch for each of the Front and Gulf or an exploitation rate, μ . Due to the short duration of the hunt this rate was multiplied by the population entering the hunt to give a catch level. The μ was assumed constant over all age classes of the 1+ population so the catch was proportional to the numbers-at-age. Also the model used only one μ for both Front and Gulf.

One complication exists with reference to mixing between the subherds during the period of exploitation if quotas are based on subarea instead of total catch. Immature harps born in the Gulf have been found in the catch in the Front area. On the basis of Sergeant's (1977) reported tag return data, the probabilities of a Gulf animal being in the Front are 0.79, 0.69, and 0.11 for 1, 2 and 3 year olds respectively (Sergeant 1977). This phenomenon was included in the model by splitting the Gulf herd according to these probabilities, subtracting the catches by area, and then returning the surviving Gulf animals on the Front to their own herd for the remainder of annual cycle.

In our annual cycle we have entered a population separated into

respective subherds and sexes and established the catch for ages, sex and subherd. However, the bulk of the hunt takes place after whelping. The herd size of 2+ animals one year earlier is used to determine the pregnancy or fertility rate. If density-dependence was not desired in a particular run the rate was set at .92 of the mature female stock. If density-dependence were desired the following equation was employed:

$$\text{Preg} = \text{CP1} + \text{CP 2} \times \text{Pop}_{2+} \text{ (lagged 1 year)} \quad (11)$$

CP1 and CP2 were determined to be 1.0293 and 7.373×10^{-8} as a best linear fit to the existing data (Eqn. 8). Also, for the sake of comparison a "steeper" set of coefficients, CP1 = 1.05 and $\text{CP2} = 9 \times 10^{-8}$ were used.

A linear relationship was also derived to relate the mean age of whelping, MAW to the population size. Analysis of the data above showed that a five year lag in the population produced the best agreement between these variables. (Eqn. 6). This relation yields the formula:

$$\text{MAW} = \text{CA1} + \text{CA 2} \text{ POP}_{t-5} \quad (12)$$

CA1 and CA 2 are read in with the starting population at the beginning of a simulation. For the 1977 population they had the values 3.875 and 9.126×10^{-7} respectively. The mean age of whelping was not allowed to shift below 4.5 years as there are no observed data beneath this value. This corresponds to limiting the ogive's translation when the population size falls to 0.8 million. The ogive describing the probability of maturity with age was sinuousoidal in shape and modeled by:

$$\text{OGIVE} = \text{SIN} (31.34 + 19.91 (\text{AGE}-\text{MAW})) \quad (13)$$

which corresponds to equation 5.

With the pregnancy rate and maturity ogive determined, the pup production was estimated as

$$\text{PUP} = \text{PREG.} \times \text{OGIVE} \times \text{FEMALE} \times 1.06 \quad (14)$$

The factor of 1.06 was included to compensate for females over the age of 25 as reported in Lett and Benjaminsen (1977). These equations are found in the block labeled "Pup production" in the Annual Cycle of Figure 7.

Previously determined catches are now subtracted from the 1+ population

and the new born pups. A natural mortality of 0.1 was then applied to 1+ animals. This parameter was treated as a stochastic variable with a standard deviation of .015. The pup mortality either had a set mean of .2 or was determined as a function of the number of pups surviving the hunt, the escapement. The function relating pup mortality to escapement was

$$\bar{M}_{\text{pup}} = -.3507 + 2.35 \times \text{escapement} \times 10^{-6} \text{ (best estimate)} \quad (15)$$

or

$$\bar{M}_{\text{pup}} = -.764 + 3.925 \times \text{escapement} \times 10^{-6} \text{ (steeper estimate)}$$

The pup mortality was constrained to a range from .03 to 0.5 as in Fig. 4. This mortality was assumed to have a related standard deviation of .03. Once the mortalities were determined the population was reduced using a simple exponential model.

$$\text{Pup} + \text{Pups} \times \text{EXP} (-M_{\text{pup}}) \quad (16)$$

$$\text{Pop}_{1+} + \text{Pop}_{1+} \times \text{EXP} (-M_{1+}) \quad (17)$$

The arrow signifies "replaced by". The population was now aged with the surviving pups replacing the 1 year olds. This is shown in the "Natural Mortality" block in Figure 7. The surviving 1 year olds became 2 year olds etc., thus finishing the annual cycle. This cycle can now be repeated to simulate the next year's population. The actual program was limited to 50 years for a given set of parameters.

Statistics on breeding population, pups born, pups surviving to 1 year old, population size, adult and pup catches were compiled for both Front and Gulf for each year. When only one stochastic run was made the mean of all stochastic variables were used in the equations. When more than one run was specified, the model was run for the requisite number of years and the statistics saved, it was then restarted from the initial values but new values for the stochastic variables were drawn and the new estimates saved again. This process was repeated over the specified number of runs and then means and standard deviations found for the breeding population, total population, pup and adult catches.

The pregnancy, whelping ogive and pup mortality had the option of operating in a density dependent manner or set to constant values. In order to demonstrate the effects of such mechanisms, projections were made with one, two or three operating. (See Figs. 8, 9, 10 and 11).

Population sizes as a function of time were projected with the hunt limited to the high Arctic and Greenland components. These variables were set at the mean values presented in Lett and Benjaminsen (1977) and were allowed to remain in all projections as they are presumed to be outside the control of management options but still must be taken into consideration.

Sustainable yields were estimated by projecting the 1977 population ahead 50 years. The catches and population sizes after 50 years were estimated for varying hunting mortalities. Such estimates are not strictly sustainable yields, as after 50 years if the exploitation rate is quite low the population and catch will still be growing where sustainable yields are defined as equilibria. But the discrepancy should be small and should decrease as the population approaches the initial population. Fortunately, the maximum of the curve (Fig. 10) is not far removed from our starting population of 1.39 million and the area of concern for management therefore is not effected by this bias. Six sets of results were compiled according to the following schedule.

Set	Whelping	Preg.	Pup Mortality	(Comment
1	variable	variable	variable	"best" estimates
2	variable	variable	variable (steep)	} for comparison to best estimates
3	variable	variable (steep)	variable	
4	variable	constant	constant	} to show effects of removing feedback loops
5	variable	variable (steep)	constant	
6	variable	variable	constant	

For all these estimates only one run was made. This is the stochastic parameters were were set at their mean values so that results represent most probable levels of the parameters for each year. If the system were linear this would result in the most probable estimate. No attempt was made to analyse the difference between the result due to the means being used instead of averaging a large number stochastic runs. However, it was

observed that the difference was less than a single standard deviation of the final value. Therefore, because of the great saving in computer time the projections were made using only one run with stochastic parameters set at mean values unless an estimate of the standard deviation was desired. The exploitation rates used to find the sustainable yields were required to yield catches of ppps: 1+ in the ratio of 80:20. For practical consideration, if a pair of rates gave any fraction greater than .195 and less than .205 they were deemed sufficient. Once a user was acquainted with the model this level of performance generally required less than 3 trials at a given level of exploitation.

RESULTS AND DISCUSSION

Results of Sequential Population Analysis

The present sequential population analysis shows the seal population dropping from a 1+ population size of 2.5 million in 1952 to 1.0 million in 1972 but recovering to 1.3 million in 1977. Numbers derived in Lett and Benjaminsen (1977) are 2.3 million in 1952 to a low of 1.0 million 1968 and recovering to 1.2 million in 1975.

Starting exploitation rates were derived using pup productions from Benjaminsen and Øritsland (1975) for the years 1966 to 1976 that came from the functional regression of pup catches on survival indices. An assumed pup mortality equal to the adult mortality was also used and the analysis was run back to age 0. For years for which both Winters' (unpublished data) and Benjaminsen and Øritsland (1975) estimate pup production, the estimates are very close. Also for years since 1966 the Y on X regression and the functional regression give values that are within 10%.

The analysis in Lett and Benjaminsen (1977) is a cohort analysis for the years 1952 and 1975. The analysis derives starting exploitation rates for 1975 and 25 year olds by averaging rates in 1973 and 1974 and ages 10-20. The cohort analysis will bias the figures but all errors will be in the same direction and should be quite small. Again pup mortality is assumed to be the same as adult mortality but this time both are assumed to be 0.114. These two differences would lead to population estimates that again show a greater proportion of young seals. Due to the sensitivity of the analysis to starting hunting mortalities, it is interesting that the 1+ population estimates agree so well with the present results even though there were no extra data used to tune the analysis.

Pup productions drop from 570,000 in 1952 to 310,000 in 1975 and rise to 330,000 in 1977. The cohort analysis in Lett and Benjaminsen (1977) produced pup productions that varied much more than this due to the way in which starting hunting mortality rates were derived. Overall, they do show the same general trend of higher values in the 1950's dropping to a low of 310,000 in 1973. The model in that paper which was derived from the cohort analysis results and other data was used to re-estimate the pup productions. This gave values of 290,000 in 1972, 310,000 in 1975 and 320,000 in 1977. Again the same trend is seen though the minimum occurs a little earlier.

The direct estimation of the number of seals in the Gulf of St. Lawrence may never be possible although fortunately other methods are available (Lett et al. 1977). Using catch and effort data we have estimated the Gulf production at about 98,000 pups between 1964 and 1971, a value which seems reasonable since the total kill of pups in the Gulf in 1971 of 72,000. Sergeant (1975) has previously stated that he feels this is very near an estimate of the total production since "ships could not get their quotas, and we could not find seals after the fishery so we could brand them". However, there was some escapement since beaters were caught in the west Newfoundland landsmen fishery on their northerly migration through the Strait of Belle Isle (Fig.1). Our estimate for total Gulf production in 1971 is 90,000 animals (Lett et al. 1977).

Discussion of the Results of Simulation

Using a numerical model and projecting ahead, our estimate of Gulf production in 1977 was 93,000 animals and in 1975, 89,000 animals (Lett et al. 1977) as opposed to Lavigne's (1975) estimate of Gulf production of 46,000. Using our estimate from the Gulf in 1977 and Lavigne et al. (1977) estimate from the Front a minimum estimate of overall production would be 303,000 pups.

Survivorship indices are available in a number of papers (Benjaminsen and Øritsland 1975; Sergeant 1975, 1976^a). It is interesting to note, however, that Sergeant (1975) estimated Gulf production in 1958 at 120,000 and in 1967 at 85,000 using the survivorship method.

Comparison to Other Models

This model could be operated with up to 3 density dependent controls. This compares with the model described in Capstick et al. (1976) which had only density dependent maturity and that of Lett and Benjaminsen (1977) which had density dependent maturity and pregnancy. The effect of increasing the number of feedback control loops is generally to stabilize the model. This stability is reflected in the ability of the modeled system to respond to changes either in environment or fishing effort. Also the incorporation of several feedbacks reduced the effect of an error in estimating a particular parameter value. This attribute is described by the sensitivity of the system which is a measure of the effect that a change in an input parameter would have on the output, say population size or sustainable yield. If the model contains a number of feedback controls it tends to reduce the sensitivity of individual input parameters and may be thought to distribute it over the rest of the model. Mohn (1977) showed an example of this in comparing the sensitivity of natural mortality in one and two feedback path models.

Qualitatively it is desirable to consider the effect of including all three feedbacks from a sensitivity point of view. The sensitivity of the model for a given parameter is generally reduced as more parameters are involved. For example increasing the pup catch could cause a response by shifting the mean age whelping, increasing pregnancy rate and decreasing pup mortality. Thus in our model the effect of an increase of 10,000 pups in the catch would be compensated by three controls and the final modeled population would be less sensitive to this change. Thus if one determined a policy from a model including these controls the results would not be as sensitive if the quota were not reached or exceeded, and updating would not be needed as often as a simpler model. Also an error in the estimation of a parameter describing the system would have a less marked effect as its sensitivity is also reduced in the more complex model. Of course there is a price to pay if a feedback control is included when the data do not warrant it. Although the individual sensitivities are reduced, the total uncertainty in the estimates produced by a model is in some sense the sum of all the individual parameter uncertainties times its effect on the estimate (its sensitivity). Adding controls for which the data are very crude may introduce more errors than a slight reduction in individual parameter sensitivities would

compensate. Therefore if data exist that indicate a feedback control mechanism, it is generally beneficial to include all such mechanisms in the simulation.

Relationship Between 1+ Stock and Pup Production

Catches of young harp seals have been higher than 600,000 and a pup production in excess of the 1952 level would be necessary to sustain the earlier levels of catch (Chafe et al. 1923). Therefore, recruitment curves were simulated (Fig. 8) under a number of assumptions to try and discern the validity of certain density-dependent mechanism.

When the age of maturity, fertility and mortality in the first year were related to population density, recruitment followed a sigmoid curve that is truncated at lower 1+ population sizes. The slight curvature toward an increased recruitment rate is a result of shifting maturity and fertility rate so that a greater proportion of the 1+ stock is capable of producing pups. As the population reaches its maximum size, under this set of constraints, of 4.3 million the whelping rate falls to 0.16. At this level the density-dependent annual pup mortality is 0.5, thus the recruitment rate of the 1+ stock is,

$$\begin{aligned} N_1 &= 0.16 \cdot \text{EXP} [-0.5] \\ &= 0.10 \end{aligned}$$

which balances the 1+ mortality.

The shape of this curve is independent of the mortality of pups since this mortality is related to the escapement from the beater hunt and not the 1+ stock. When the fertility is held at 0.92, a long term average value, and annual natural mortality of pups is held at 0.2, the resulting recruitment curve diverges from that with all 3 density-dependent mechanisms operating, at a 1+ population size of 2.2 million (Fig. 8).

When only the maturity ogive is allowed to shift the whelping rate at a population size of 3.74 million seals is 0.20 compared with that at the equivalent 1+ stock when all density-dependent mechanisms are operating of 0.18 (Fig. 8). Thus a mechanism that regulates the mortality of pups has quite a dramatic effect on the rate of recruitment to the 1+ stock and the maximum size the population can achieve. It would seem that Sergeant's statement that pups represent between 0.20 and 0.25 of the total population is slightly in error. This study indicates that between 0.16 and 0.22 of the total population can be pups.

It is important to note that under equilibrium conditions a so-called

"stock-recruitment" relationship for harp seals does not have a descending right hand limb. Lett and Benjaminsen (1977) state that for a stock as undynamic as harp seals it is impossible to have a declining portion of a recruitment curve since this means the population is much further out of equilibrium with the carrying capacity of the environment than it is possible for seals to become. Thus recruitment does not follow either the Beverton and Holt (1957) or Ricker (1954) recruitment curve, although as Allen (1975) has pointed out, fitting either curve would not greatly jeopardize management decisions over a wide range of stock sizes. Allen (1973) shows a similar recruitment structure for fin whales (*Balaenoptera physalus*) although it is not clear from his raw data whether the shape is due to a changing population structure or a shift in maturity. In general, it would seem that a truncated sinusoidal function would best describe the data. In general, the model fits the data from sequential population analysis quite well (Fig. 8) with the autocorrelative nature of the points being a result of a fluctuating population structure. However, over the time series of biological sampling the population has never been large enough to say which of the two recruitment curves is superior.

Maximum Population Size

It has previously been stated by Sergeant (1975) that the maximum population size may have been near the 1952 level because of the poor condition of molting adults. This study indicated that 1+ population size, no matter what set of assumptions are made achieves at least 4 million seals, as compared with 2.5 million in 1952 from our sequential population analysis. However, the assumptions about the factors controlling the dynamics of the population severely affect estimates of virgin stock size (Fig. 9). When no density-dependent mechanisms are operating the population increases continuously at a rate of 9% per year. Density-dependent pup mortality does not seem to constrain the population within a reasonable level either. Using only this mechanism the population continues to grow at about 4% per year.

Either a density-dependent fertility rate or whelping rate will cause the growth of the population to become asymptotic when operating independently. The maximum population size under the density-dependent fertility alone is about 10 million (Fig. 10) somewhat higher than that estimated in Lett and Benjaminsen (1977). However, maximum population size here depends upon other assumptions made concerning mean age of whelping and mortality in the first year. Density-dependent whelping

alone constrained the population to about 8 million animals. Thus it can be concluded that of the three density-dependent mechanisms, that controlling the age of whelping has the greatest control over fluctuations in population size.

When both density-dependent whelping and fertility operate together, the maximum population is about 5.5 million. Lett and Benjaminsen (1977) found that under a similar set of assumptions that the population size never exceeded 4.1 million. However, the circumstances under which the Lett and Benjaminsen model was run are different than in the current situation. In Lett and Benjaminsen model the landsmen and high arctic hunt continued to operate, and only the large vessel hunt was discontinued. In this case all hunting is terminated except the small high arctic hunt which is considered part of natural mortality by some modellers (Capstick et al. 1976). When all three density-dependent mechanisms operate the maximum population size including a small high arctic kill is 4.2 million seals.

Production Curves and Density-Dependence

The fitting of general production models to data, whether it be catch as a function of average exploitation rate, or the total population size from sequential population analysis gives poor statistical relationships. Indeed, our efforts resulted in a coefficient of determination of only 4%. We then ran a small experiment with simulated data. Using the model with density-dependent mechanisms operating, four lots of data were generated each consisting of fifty ordered pairs of 1+ population size and total catch. An approximate ratio of 80% to 20% pups were used. The exploitation rate was assumed to follow a sine function with an associated variance.

$$\mu = [\sin (\pi/50 t) + \Sigma] C_1 + C_2 \quad (18)$$

where C_1 and C_2 were chosen so that μ pups oscillated between 0.1 and 0.55. A second pair of C_1 and C_2 yielded μ_{1+} between 0.004 and 0.036, Σ is a random normal variate of zero mean and standard deviation 0.1. Exploitation rates were constrained between zero and 1.1 times the upper level. The data were fitted using Gulland's (1961) technique with a 5 year running average. The maximum sustainable yield, MSY was 196,000 seals and the corresponding population size 1.71 million. When all 100 points are used the MSY was 179,000 and corresponding population size 1.61 million. For this set of conditions in the complete model, MSY is 215,000 animals for a corresponding population size of 1.4 million (Fig. 11). This constitutes at least a 9% error in the estimation of MSY and 18% error in MSY

population size.

When only the density-dependent maturity was included in the simulation Gulland's model could not be fitted to the first 50 years of data since the slope on the autocorrelative function of catch per unit population vs population was positive. By adding another 50 points the MSY was determined to be 250,000 for a population size of 3.4 million. The corresponding 'best' values are 255,000 and 3.1 million. This study, although somewhat reliant on our initial assumptions indicates that fitting production models can lead to serious errors especially in the determination of MSY stock size. Furthermore, the MSY using a linear procedure merely gives an estimate of the mean catch. A non-equilibrium, stochastic method was almost as poor (Schnute 1977); however his method at least gives an indication of its ineffectualness.

It is our belief that the general production relationship should be generated from the basic biological relationships governing the dynamics of the stock through the use of stochastic simulation methods. If the basic relationships are understood and accepted, then, and only then, are equilibrium relationships of any use in managing the stock (Figs. 10 and 11).

A general production curve can be generated by the simulation by running the model at a specific exploitation rate on pups and 1+ seals and then taking the mean and standard deviations of a set number of stochastic runs which have reached an equilibrium or a stable limit cycle. Usually it takes as long as fifty years before an equilibrium level is reached. For this study the ratio of the kill of pups to adults is always 80:20 since this is a ratio that has been maintained over the last decade. Of course the results depend upon this ratio; a higher fraction of pups would lead to larger MSY's.

The degree of density-dependence has a profound effect on the shape of the curve and the determination of MSY (Fig. 11). Two different relationships for density-dependent fertility were used in addition to allowing the maturity ogive to vary in response to population size. In one relationship the rate of change of fertility in response to population was 20% greater which is well within the range of possibilities (Fig. 6). The alteration did not have that much effect on the MSY which only dropped from 230,000 to 225,000. It is also interesting to study the effect of a density-dependent fertility on the equilibrium catch at stock sizes below MSY. In the case of the harp seal higher fertilities than those occurring an average (0.92) increase the surplus yield.

Lett and Benjaminsen (1977) using a similar procedure indicate that the MSY is about 240,000 animals for a population size of about 1.6 million, while a recent update of the model (Lett et al. 1977) indicates that the MSY population size is near 1.5 million. The basic difference between the two models is the estimate of natural mortality, 0.114 in Lett and Benjaminsen (1977) and 0.10 in Lett et al. (1977). Thus a drop in natural mortality leads to lower MSY (240,000 to 220,000) and a drop in MSY population size. In the model discussed here mortality on pups has again been raised to 0.2, thus MSY stock size is now 2.5 million, but the MSY lies between the other two levels at 230,000. In all cases the ratio of pups to adults is 80:20. One further consideration when comparing the three models is, that when an assumption changes altering fundamental values, such as numbers at age, all the other parameter values in the model must also change accordingly. Thus some of the discrepancies in the different levels of MSY and MSY population size are due to changes in the rate at which whelping and fertility respond to population size, or in general terms the degree of density-dependence.

When all three density-dependent functions were allowed to vary the MSY dropped slightly to 215,000, the MSY population size dropped quite dramatically to 1.4 million, the curve became skewed toward higher population sizes and the MSY became much better defined (Fig. 10). The shape of the curve is due primarily to the hypothesized relationship between escapement and pup mortality (Fig. 4). At low stock sizes the escapement is low and therefore the mortality of pups is less than 0.1. Thus the production function rises very quickly to an MSY level. However, then the full effect of the rapid increase in natural mortality comes into effect increasing the rate of decline of the right hand limb (Fig. 10). But once the escapement becomes greater than 300,000 the effect of density-dependent natural mortality levels out at a value of 0.5 and the curve skews toward higher stock sizes.

Around the area of MSY, a 57% increase in stock size only leads to a 16% change in yield (Fig. 11). Thus within the confidence limits of our data it is very difficult to determine a stock size that will yield MSY. This analysis indicates that for harp seals the determination of an MSY stock size we do not have enough confidence in our basic data and sub-models to aim at an MSY stock size as viable management objective. The question is then how should the stock be managed in relation to this kind of variability and uncertainty.

Density-Dependence, Variability and the Formulation of Management Strategy

The problems of environmental variability in relation to general production models and in particular the Schaefer (1954) model were first discussed by Doubleday (1976). Later Sissenwine (1977) repeated and somewhat refined Doubleday's original work. Independently, Beddington and May (1977) and colleagues have considered a similar problem and have applied it to specific animal populations.

Lett and Benjaminsen (1977) have commented on the biological basis for increase in the variability of catch associated with a decrease in stock size (Fig. 10). Variance in the present model is a result of fairly uncontrolled landmen as a result of ice conditions and high arctic hunt. Furthermore, the uncertainties associated with natural mortality are incorporated but this does not contribute much to the overall variance (Mohn 1977). Although one would generally expect density-dependent mechanisms to stabilize a system this is offset to a degree by the uncertainty in the parameters defining the controls.

One of the problems investigated in this study was the effect of the number of feedback controls i.e., density-dependence, operating on the coefficient of variance of the MSY. In fact, the number of density-dependence mechanisms did not effect the coefficient of variance in any consistent manner. However, our findings may be a result of the way in which we conducted the study. It is an area that should be the subject of more research.

Doubleday (1976) and Beddington and May (1977) all indicate that a stock below the MSY level stands a better chance of collapsing than one above the MSY level. Furthermore, it is better to harvest at a constant exploitation rate than at a constant quota level since at a constant level stock sizes, which fall below a sustainable yield level, can never recover. Even when harvesting harp seals at a constant exploitation rate for a population size less than 800,000 animals there is a good probability that the stock will collapse through natural fluctuations (Fig. 10). Based upon the model presented here this perhaps can be defined as a critical stock size.

Critical stock size for harp seals is the point at which certain density-dependent mechanisms cease to operate. Most density-dependent mechanisms are the result of varying amounts of surplus energy affecting the physiology of the animal. If a harp seal can gather, eat and digest no more food than it is already gathering the density-dependent mechanisms no longer can have any effect on the population dynamics.

For harp seals the minimum mean age of maturity is about 4.5 years, and no harp seal population has ever been observed to have a fertility greater than .98. Both upper biological limits are reached for a stock size of about 800,000 animals. At this point any factors leading to lower population sizes cannot be compensated for at constant level of exploitation. If recruitment is not known and varies widely this is indeed a severe problem.

For some mammal stocks recruitment can be easily calculated from current stock size which is quite well understood. In these cases knowing where the MSY stock size lies is not that important, in fact not even that relevant if it does not correspond to some socio-economic optimum or maximum. Perhaps a good management strategy is to allow the stock to slowly build to a point where someone can find some legitimate reason why it should build no further. Some people have suggested that the seal stock should be constrained because they will compete with fishermen for the available resource. However, we are quite sure that when the harp seals begin to interfere with fishermen we will hear about it.

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Table 1. Catch-at-age data from 1974 to 1977. Catch-at-age data from 1952 to 1974 are available in Lett and Benjaminsen (1977).

Age	1974	1975	1976	1977
0	118036	140629	132085	124932
1	9604	9629	10928	5448
2	5629	5719	6241	4898
3	2123	3275	3976	4271
4	1752	1999	2874	3154
5	1945	2072	1567	1677
6	3144	1867	1264	1163
7	985	1832	1073	921
8	1200	1186	1027	743
9	1283	740	481	357
10	954	693	757	236
11	732	672	523	259
12	891	605	369	161
13	825	646	306	266
14	685	529	309	368
15	674	353	517	335
16	686	350	191	64
17	594	247	221	35
18	447	323	145	131
19	377	159	135	29
20	306	127	155	128
21	282	88	40	50
22	287	106	46	35
23	201	59	53	29
24	219	97	31	27
25	210	74	30	22
1+	36035	33447	33259	24817

Table 2. Pup productions derived from sequential population analysis compared with those derived by Winters (unpublished data) from survivorship indices.

YEAR	DERIVED	WINTERS	(90% CONFIDENCE LIMITS)	
1952	566323	666000	(477000	2127000)
53	550422	530000		
54	555380	549000		
55	554578	572000		
56	557712	531000		
57	556217	528000		
58	547560	517000		
59	512450	495000		
1960	493828	492000		
61	464710	483000		
62	430747	466000		
63	401433	423000		
64	379204	380000		
65	360720	397000		
66	363435	395000		
67	357433	393000		
68	362502	406000		
69	368569	390000	(332000	497000)
1970	361750	381000		
71	348087	379000		
72	330996			
73	330520			
74	318239			
75	308931			
76	313517			
77	330000			

TABLE 3 : NUMBERS FROM SEQUENTIAL POPULATION ANALYSIS

Year Age	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964	1965
1	211989	207052	210497	184239	163758	201306	170463	169800	189984	234573	247556	146708	191684	166069
2	255436	187582	188632	158657	143176	134905	159087	113640	130858	137658	206291	199035	128612	171179
3	269909	220696	163826	139809	132250	123059	111394	125216	92169	101919	122208	155756	172145	110566
4	183522	237357	194366	144384	119695	115850	103349	89184	107261	74252	89898	101827	133656	150005
5	140226	160644	211229	170039	125697	105269	100048	85020	64331	75998	64331	72703	87631	114215
6	305596	120661	141748	187879	149571	111328	91407	82236	72984	62904	79086	51778	61971	74438
7	102839	265630	106277	124453	166481	133247	97434	75246	70938	60806	55710	68907	42713	49104
8	145309	85406	237780	92653	109563	148731	117621	81998	65041	59774	53820	47714	58451	34923
9	97301	123969	74754	212120	80967	97286	131946	100756	71462	55051	53352	45910	39238	49795
10	125841	82713	109700	65608	189592	171630	85659	114552	88697	11280	49115	45594	37928	32619
11	96067	107793	72794	96301	57180	170113	62557	72775	101402	77084	54370	43219	37109	30020
12	66238	81596	95055	66646	85183	50492	151857	52303	63887	88907	69104	47873	35089	31228
13	102265	58378	72326	83439	56656	75856	43798	133670	45551	55187	80076	60650	40357	29448
14	61374	91147	51676	62904	73903	50207	66939	36198	119328	38839	49564	71406	51766	34686
15	72773	53430	81572	45465	55417	65864	43792	57475	31178	105721	34779	43445	61388	45041
16	135448	62040	46618	72106	39720	49271	58085	36783	50563	26163	95476	29371	36751	53013
17	20453	121253	54416	39996	63901	35030	43188	50048	31944	43786	23379	85657	24549	31160
18	18216	16376	108452	48250	35004	57035	30460	36756	44092	27174	39395	19499	75375	19600
19	19157	14814	14022	97778	42608	30890	50517	25581	32328	38382	24470	34819	16267	64321
20	19213	16463	12825	11563	87507	37889	24944	43976	22174	27778	34587	21552	30381	12609
21	12876	12887	12376	10930	9685	78615	33411	22805	39019	18912	24960	29966	18319	27362
22	5679	10399	10185	10876	9280	8357	70504	29191	20077	34470	17064	22419	26113	14595
23	28075	5084	8587	8910	9305	8042	7005	62864	25917	17414	31095	14794	19503	22605
24	14991	24968	4013	7070	7684	8129	6899	5576	56495	22894	15686	27956	12737	16625
25	19396	12348	22168	3495	6083	6715	7020	5608	4735	50655	20656	14028	24783	10063
1+	2530208	2380687	2286094	2143570	2019865	1975117	1873385	1709260	1653991	1610054	1636029	1502585	1462517	1395289
2+	2318219	2173635	2075398	1959330	1856107	1773811	1702922	1539460	1464007	1375481	1388473	1355878	1270833	1229220
Year Age	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977		
1	113727	88140	82823	211945	101990	99200	139219	239673	213299	210180	211166	190463		
2	143558	92446	69910	69530	172788	85187	83147	125075	215102	184311	181466	181183		
3	151548	120502	79034	59167	60205	149527	74834	74068	110572	189539	161597	158550		
4	95612	132436	107262	68736	50742	52020	132953	65656	64747	98129	168538	142621		
5	129932	81615	117942	95405	59922	43521	46017	118878	57520	57001	86982	149899		
6	96207	112247	70602	105196	83642	52060	38248	40187	104519	50286	49702	77286		
7	60705	81545	97258	62335	93263	74156	46414	33667	35238	91728	43812	43828		
8	41607	50066	69857	85798	54160	82781	66551	41255	29288	30993	81341	38672		
9	29948	34442	42534	60949	74934	47525	74413	59537	36081	25415	26971	72671		
10	44079	25272	29149	36943	53045	65953	42300	66735	52745	31486	22327	23969		
11	28136	38139	21211	24786	31771	46226	58919	37513	59445	46863	27863	19517		
12	26571	23176	32445	18007	20920	27584	41325	52776	32684	53126	41795	24738		
13	26367	22453	19550	28425	15250	17724	24411	36856	46524	28167	47523	37484		
14	26048	22375	19126	16806	24548	12736	15594	21588	32241	41350	25445	42724		
15	29980	21918	18570	16190	14001	21448	11273	13788	18571	28553	36936	22744		
16	39475	25728	18195	15824	13389	19104	9830	11511	16194	16194	25517	32953		
17	47250	34288	22113	15525	13421	11288	10203	17011	8072	9795	14336	22916		
18	27732	41755	29248	19192	12918	11377	9957	8993	14775	6766	8639	12772		
19	16970	23628	36341	25346	16425	10983	9972	8806	7573	12965	5830	7686		
20	57330	14418	19924	31912	21991	14226	9711	8880	7492	6512	11587	6512		
21	11102	50884	12012	17357	28036	19286	12581	8559	7523	6503	5777	10344		
22	24221	9340	45423	10430	15090	25016	17267	11264	7475	6552	5804	5191		
23	12951	21601	8006	40482	13372	22371	22371	15539	9568	6504	5832	5210		
24	20401	11097	19046	6902	36185	7918	11892	20187	13879	8476	5831	5229		
25	14964	18123	9679	16992	6003	32565	7048	10711	18129	12360	7581	5248		
1+	1316494	1197633	1097261	1160179	1083577	1035359	1025730	1147034	1214571	1260350	1310197	1339052		
2+	1202692	1109493	1014438	948233	981587	936052	886511	907361	1001272	1050170	1099031	1148588		

Table 4. Assumed terminal exploitation rates, 1+ and 11+ exploitation rates derived from sequential population analysis and the ratio of the inputted rates to the 11+ rates.

YEAR	AGE 25	AVE. 1+	AVE. 11+	$\frac{25}{\text{AVE. AGE } 11+}$
1952	.025	.058	.066	.378
53	.021	.045	.054	.384
54	.014	.041	.038	.384
55	.013	.040	.035	.385
56	.009	.026	.023	.383
57	.012	.039	.032	.381
58	.022	.076	.059	.378
59	.011	.041	.029	.377
1960	.015	.060	.039	.373
61	.002	.012	.006	.369
62	.010	.049	.028	.366
63	.019	.058	.052	.364
64	.025	.069	.069	.367
65	.009	.035	.024	.359
66	.017	.055	.048	.359
67	.019	.054	.053	.358
68	.014	.040	.040	.357
69	.018	.049	.051	.355
1970	.015	.041	.043	.354
71	.007	.021	.019	.354
72	.006	.017	.016	.353
73	.016	.038	.045	.352
74	.012	.032	.033	.352
75	.006	.022	.017	.351
76	.004	.017	.011	.350
77	.004	.012	.008	.528

Table 5. Catch distributions and sex ratios as a function at age.

Age	Landsmen Front	Landsmen Gulf	Large Vessel Front	Large Vessel Gulf	Greenland	High Arctic	Initial Sex Ratio % ♀	Sex Ratio Large Vessel Cat % ♀
1	.120	.034	.300	.034	.306	.131	.50	.47
2	.100	.081	.134	.081	.185	.160	.50	.47
3	.090	.122	.080	.122	.125	.212	.50	.41
4	.090	.106	.060	.106	.084	.116	.50	.36
5	.060	.093	.050	.093	.058	.083	.50	.31
6	.070	.089	.040	.089	.042	.062	.50	.27
7	.060	.079	.040	.079	.031	.046	.50	.24
8	.050	.066	.030	.066	.024	.037	.51	.21
9	.050	.050	.030	.050	.018	.029	.51	.19
10	.040	.047	.030	.047	.015	.023	.51	.17
11	.040	.039	.020	.039	.013	.018	.51	.16
12	.030	.035	.020	.035	.011	.015	.52	.15
13	.030	.023	.020	.023	.010	.013	.52	.15
14	.020	.022	.020	.022	.009	.010	.53	.15
15	.020	.022	.020	.022	.008	.008	.53	.15
16	.020	.013	.020	.013	.007	.007	.56	.15
17	.020	.015	.020	.015	.007	.006	.59	.15
18	.010	.014	.010	.014	.007	.005	.59	.15
19	.010	.008	.010	.008	.006	.004	.62	.15
20	.010	.019	.010	.019	.006	.003	.57	.15
21	.010	.007	.010	.007	.006	.003	.63	.15
22	.010	.005	.010	.005	.006	.003	.60	.15
23	.010	.005	.010	.005	.006	.002	.74	.15
24	.005	.003	.005	.003	.005	.002	.69	.15
25	.005	.003	.001	.003	.005	.0	.81	.15

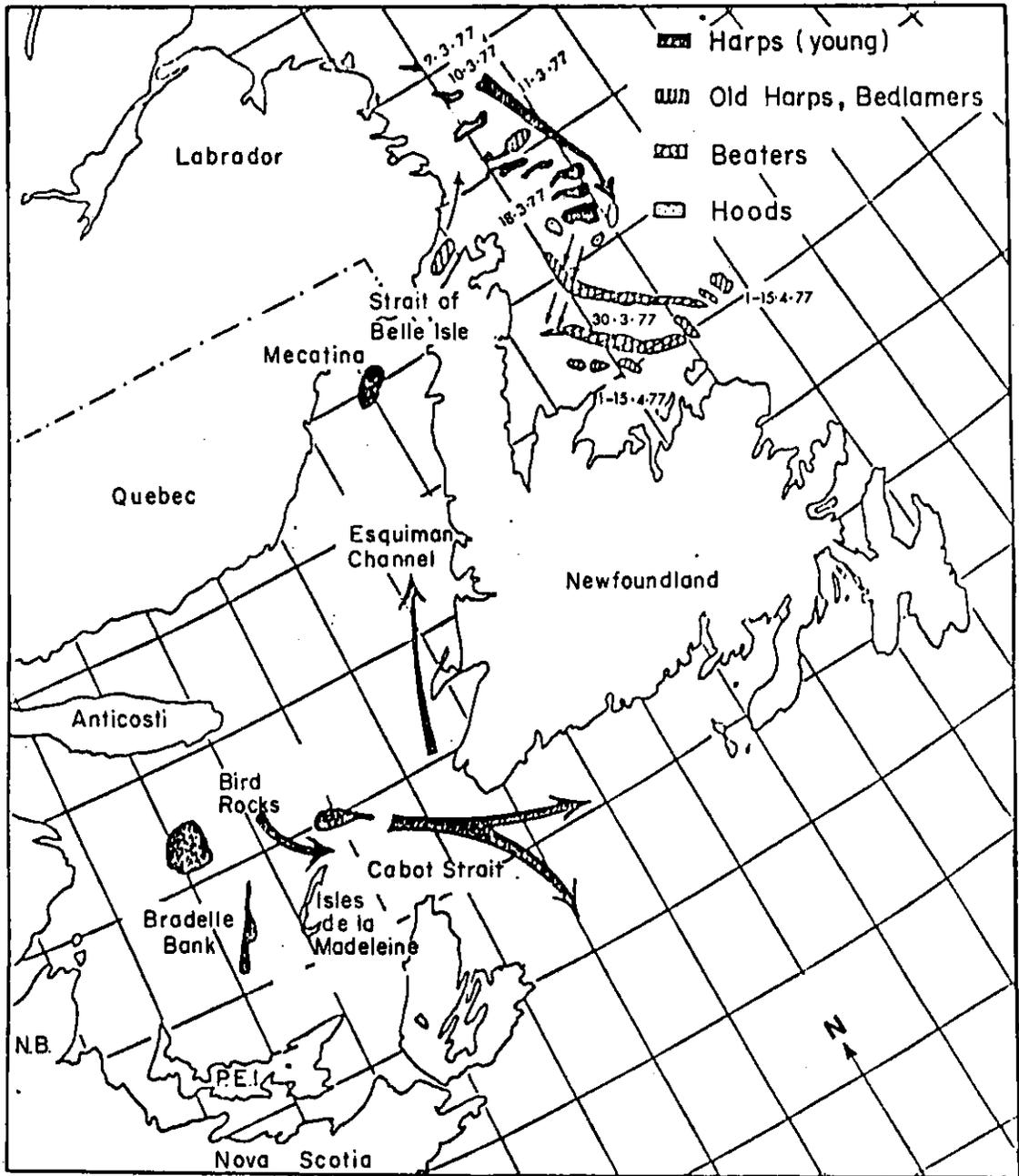


Fig. 1. Map showing movement of harp and hood seals in the Northwest Atlantic.

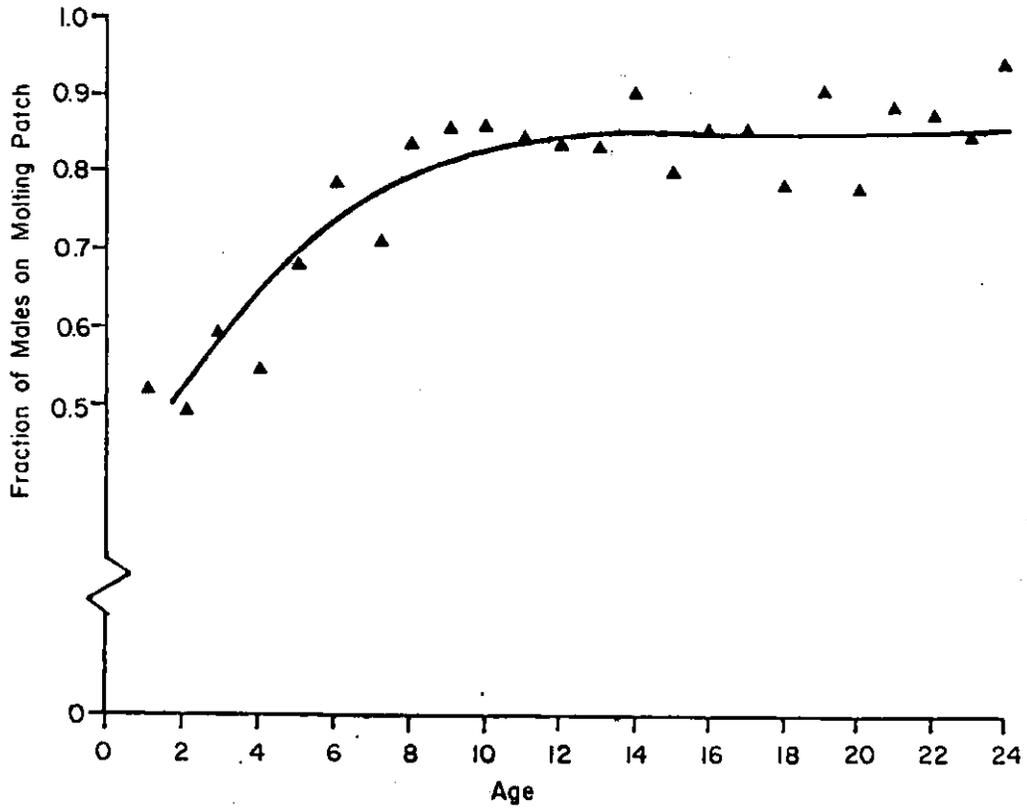


Fig. 2. The fraction of males in the Norwegian catch of molting Northwest Atlantic harp seals from 1969 to 1974 (from Benjaminsen and Øritsland, 1975).

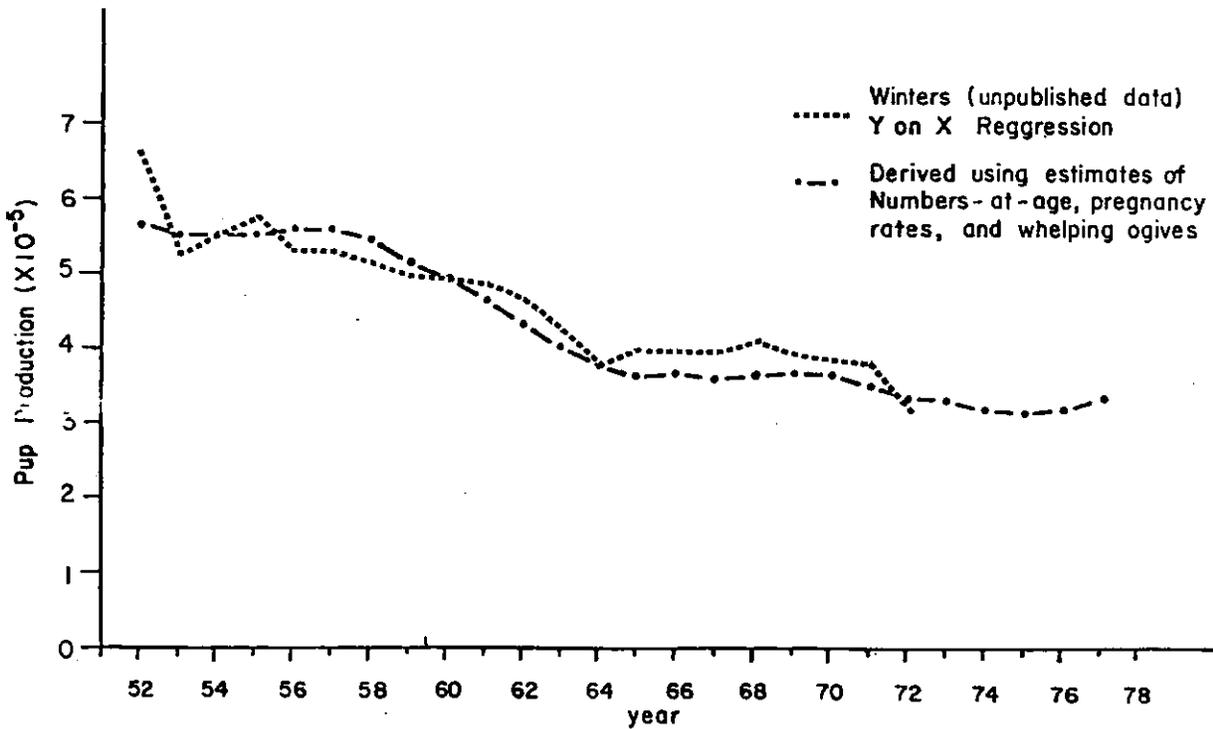


Fig. 3. Pup production from sequential population analysis versus pup production from Winters (unpublished data - Y on X regression values).

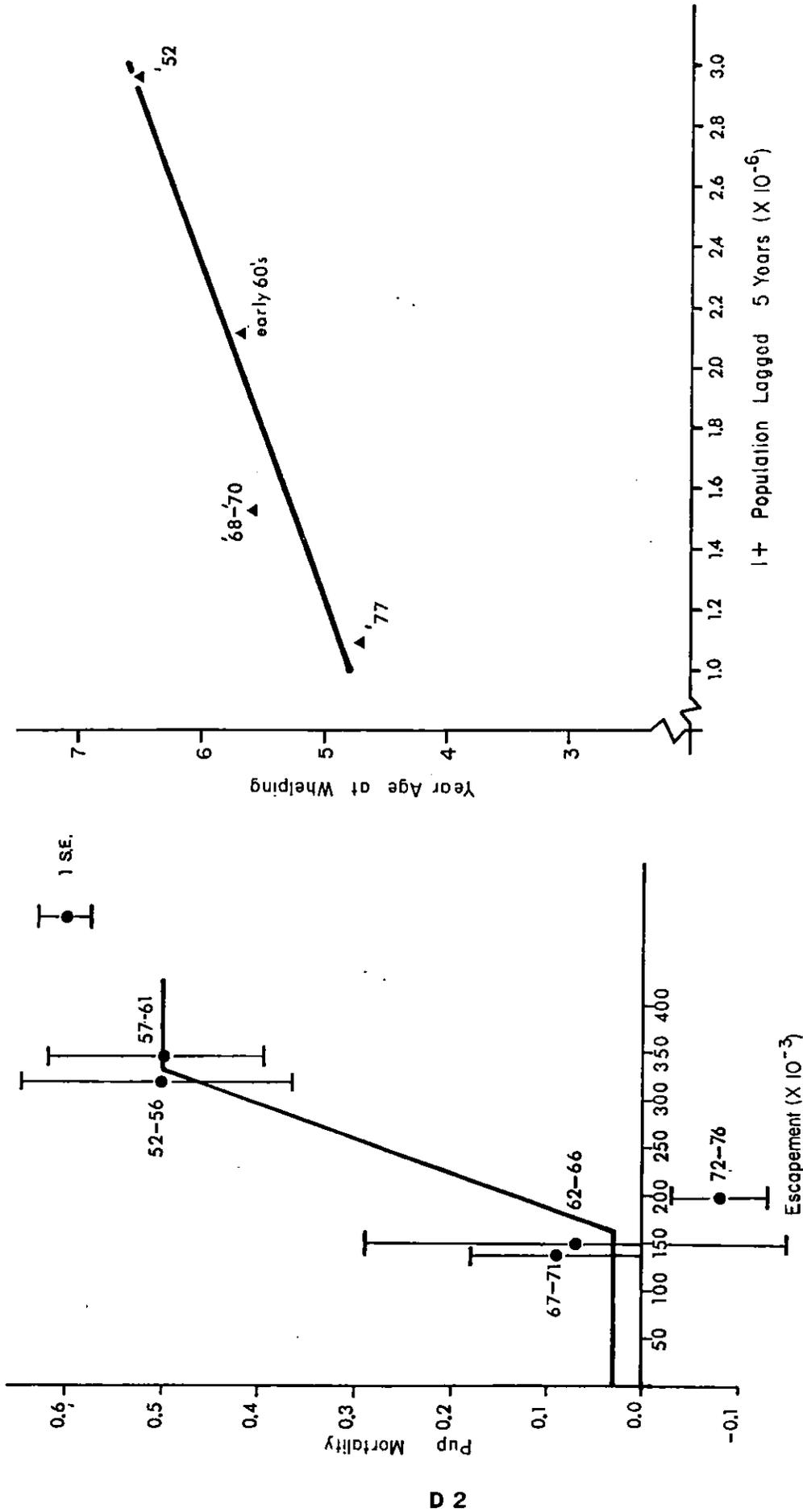


Fig. 5. Mean age at whelping as a function of the 1+ population five years before.

Fig. 4. Pup mortality as a function of escapement.

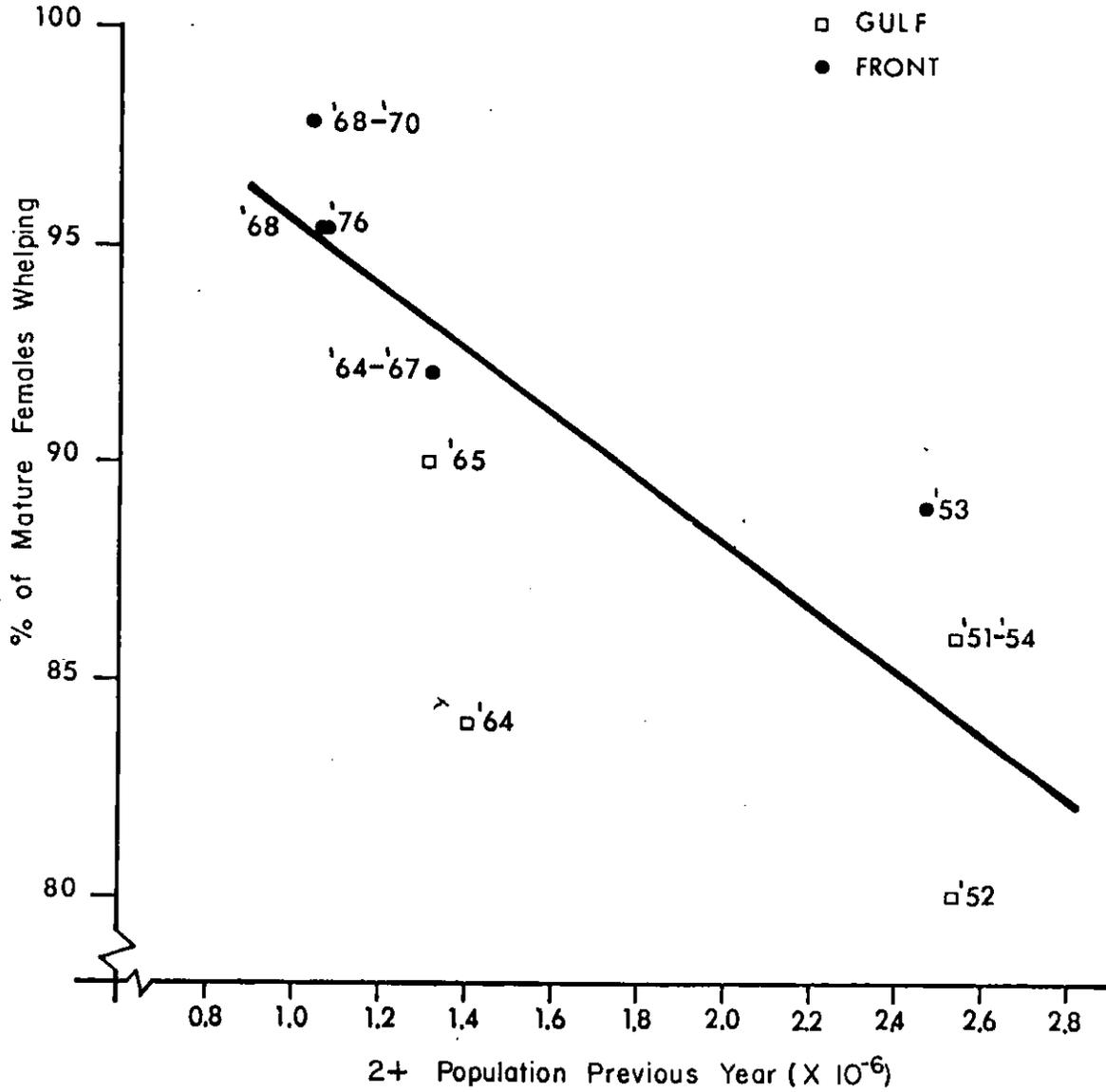


Fig. 6. Percent of mature females that whelp as a function of the 2+ population the previous year.

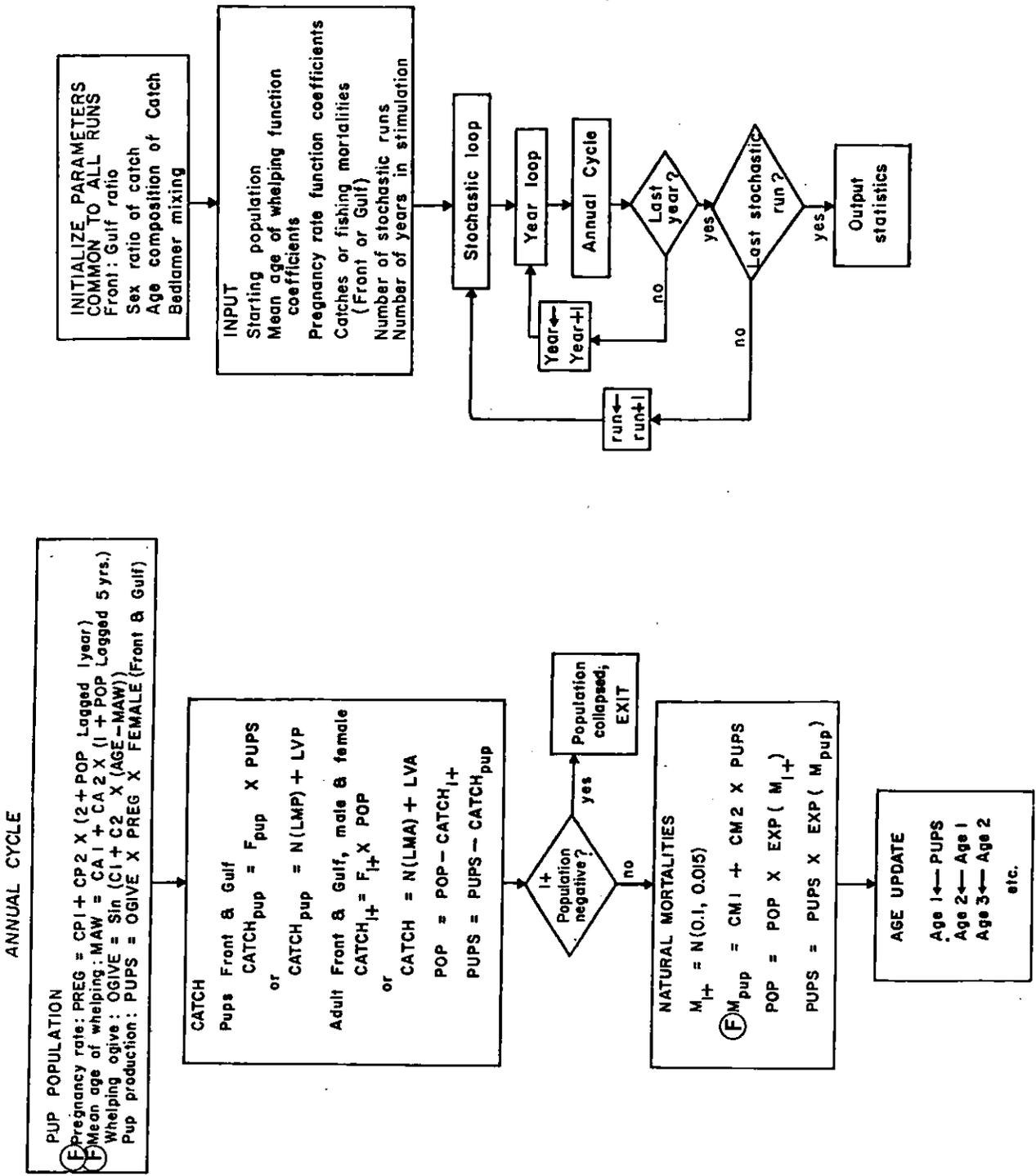


Fig. 7. Flow chart of harp seal production model and details of its annual cycle.

Fig. 7. (cont'd). Flow chart of harp seal production model and details of its annual cycle.

(F)	Feedback Controls
POP	1+ Population
PREG	Pregnancy rate - proportion of mature females that become pregnant
CP 1	Constant term in pregnancy rate function
CP 2	Linear term in pregnancy rate function
MAW	Mean age of whelping
CA 1	Constant term in mean age of whelping function
CA 2	Linear term in mean age of whelping function
OGIVE	Whelping ogive - proportion of females of a particular age that can potentially whelp
Sin	Sine function - argument constrained between 0° and 90°
C1	Constant term in whelping ogive function
C2	Linear term in whelping ogive function
AGE	Vector of ages
PUPS	Number of pups produced
FEMALE	Vector of number of females of each age
CATCH _{pup}	Pup catch - separate values for Front and Gulf
F _{pup}	Fishing mortality rate on pups
N(a,b)	A draw from a normal distribution with mean 'a' and standard deviation 'b'
LMP	Mean and standard deviation of landsman pup catch - separate values for Front and Gulf
LVP	Large vessel pup catch - separate values for Front and Gulf
CATCH ₁₊	Adult catch - separate values for male and female, Front and Gulf
F ₁₊	Fishing mortality rate on adults
LMA	Mean and standard deviation of landsman adult catch - separate values for male and female, Front and Gulf
LVA	Large vessel adult catch - separate values for male and female, Front and Gulf
M ₁₊	Natural mortality rate on adults
M _{pup}	Natural mortality rate on pups
CM 1	Constant term in pup mortality function
CM 2	Linear term in pup mortality function
EXP	Exponential function

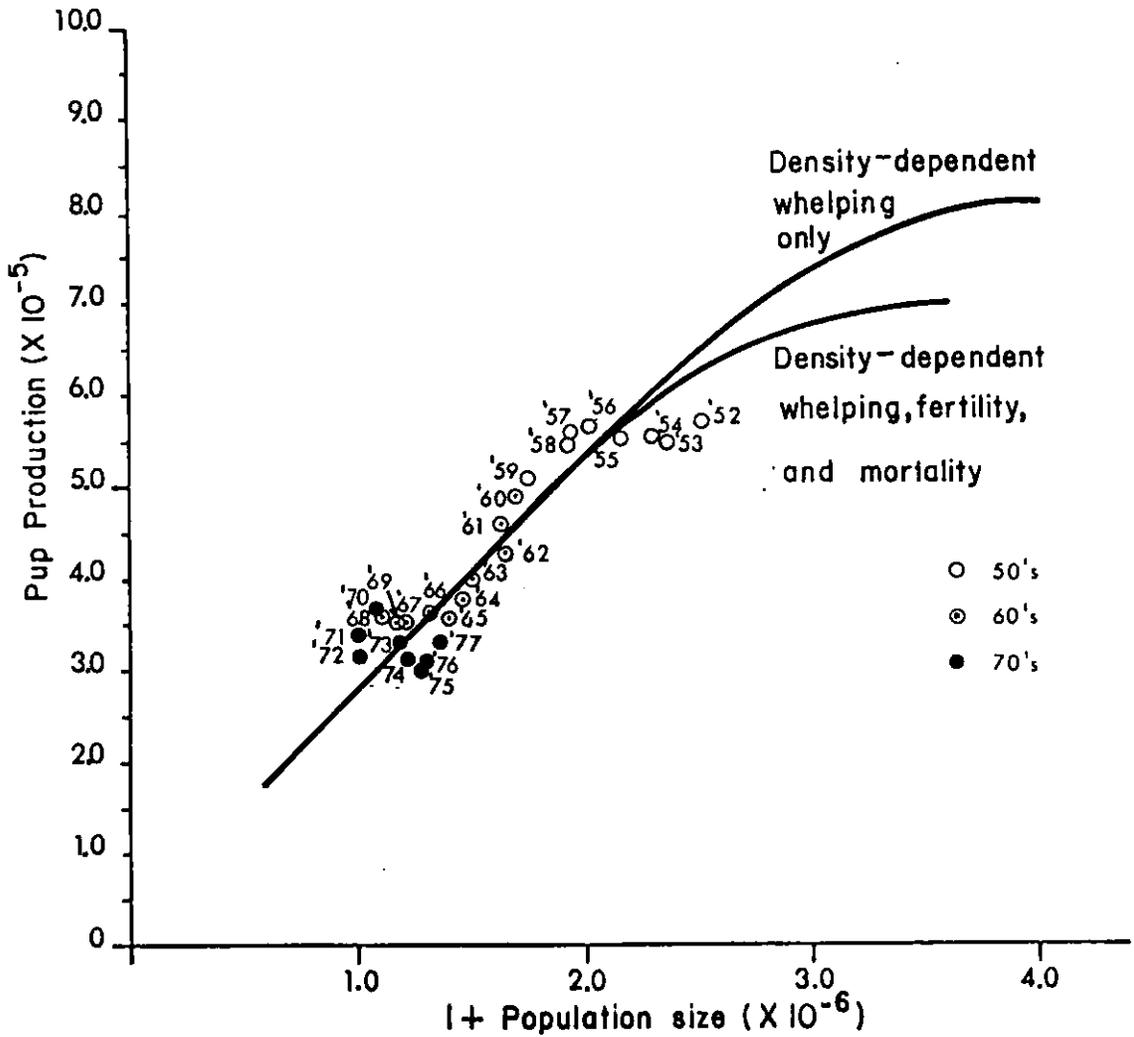


Fig. 8. Pup production as a function of population size; historical data and simulated output.

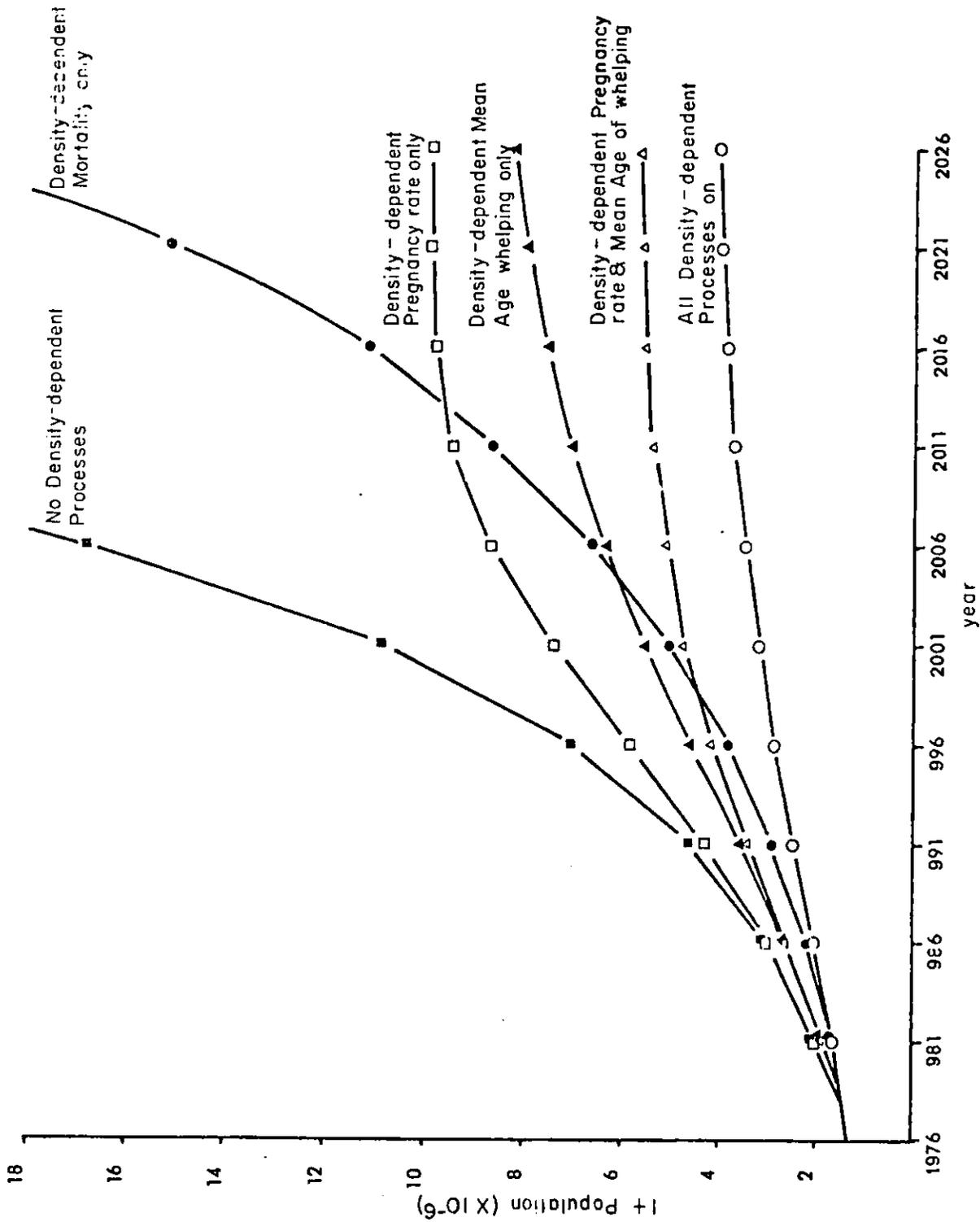


Fig. 9. Projected population size as a function of time with only high Arctic and Greenland catches for various combinations of density-dependent controls.

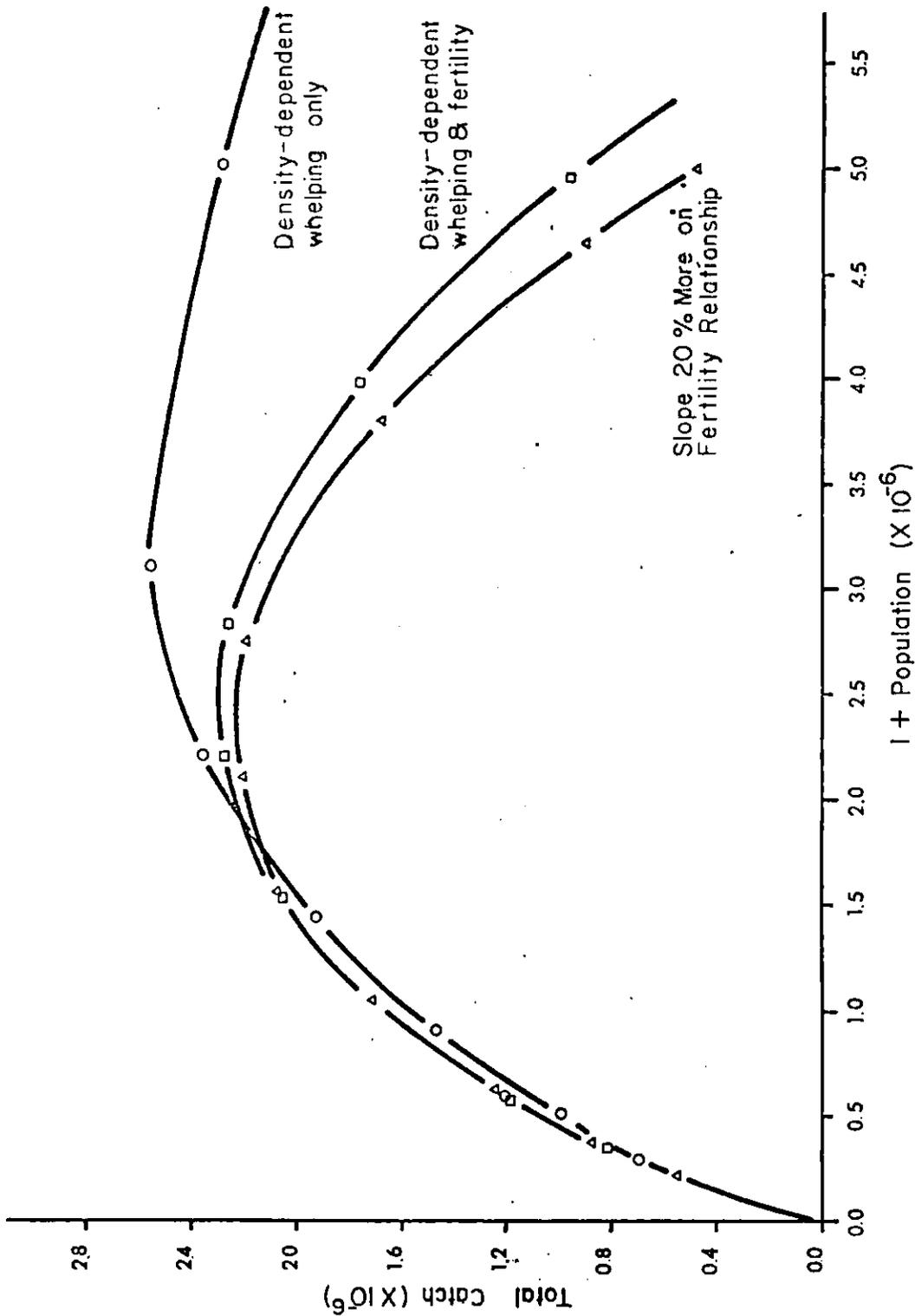


Fig. 10. Sustainable yield estimates with three density-dependent mechanisms. Circles are from the best estimates of coefficients in the mean age of whelping, pregnancy and pup mortality equations. Triangles and squares have respectively steeper pup mortality and steeper pregnancy relationships representing stronger controls. Graph also shows two standard deviations for several points. Dashed lines are estimate of two standard deviations at points where population sometimes collapsed.

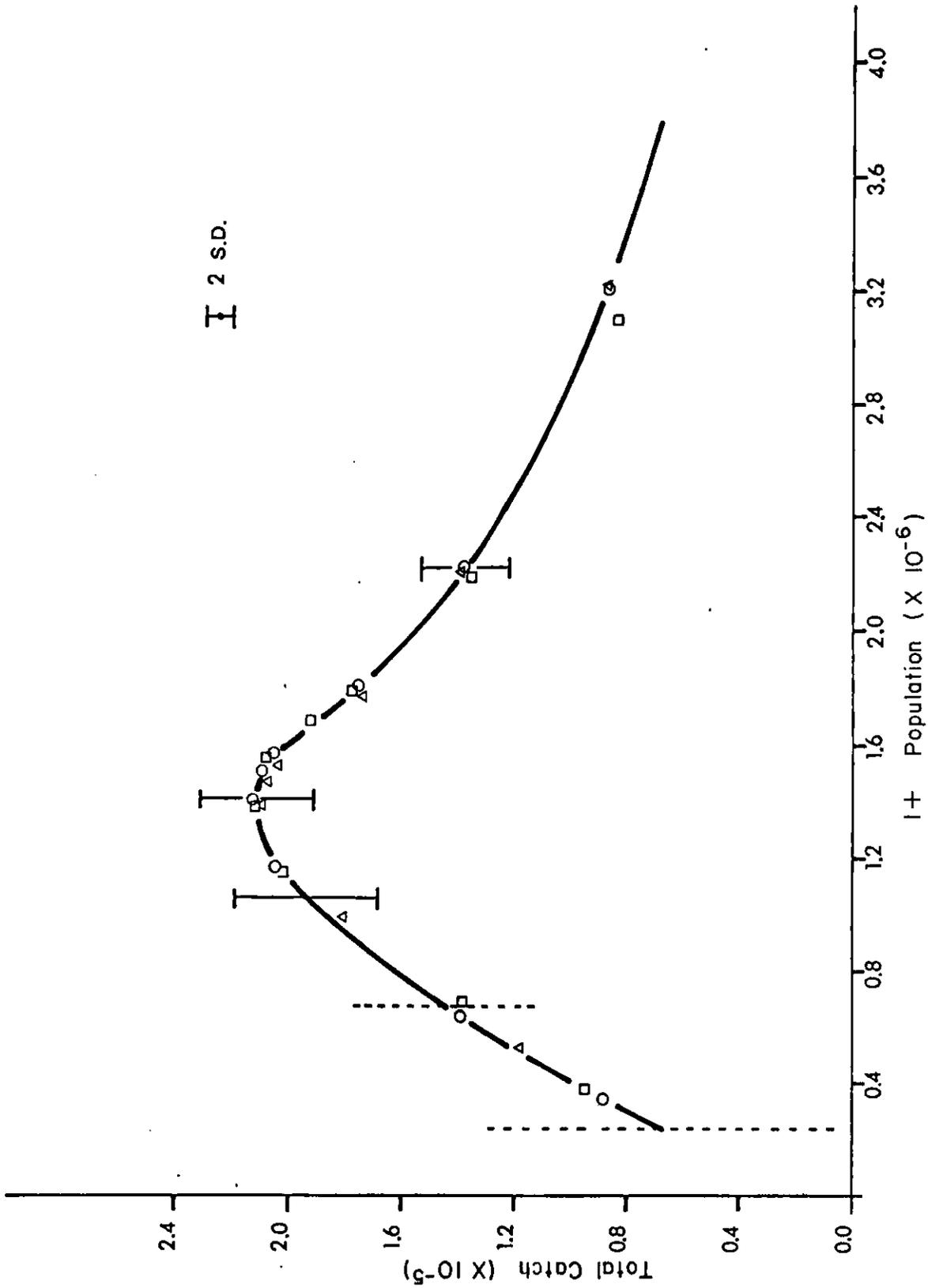


Fig. 11. Sustainable yield estimates with two and one density-dependent mechanisms. Circles have only density-dependent mean age of whelping, and pregnancy rate is a constant 92%. Triangles and squares have both density-dependent mean age of whelping and pregnancy rate. Triangles have a steeper slope in the pregnancy rate relation. Pup mortality is 0.2 in each case.